VIE ET MILIEU - LIFE AND ENVIRONMENT, 2015, 65 (4): 1-10

VARIATION OF GROWTH PERFORMANCE OF THE STRIPED VENUS CLAM *CHAMELEA GALLINA* (MOLLUSCA: BIVALVIA) (LINNAEUS, 1758) IN RELATION TO ENVIRONMENTAL VARIABLES ALONG THE SOUTHERN PART OF ITS GEOGRAPHIC RANGE

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CHAMELEA GALLINA
RELATIVE GROWTH
AGE
HUELVA COAST
OVERALL GROWTH PERFORMANCE
PHI PRIME
ENVIRONMENTAL SETTINGS
GEOGRAPHICAL DISTRIBUTION

ABSTRACT. – This study reports relative growth, shell length-age keys and growth performance indices (overall growth performance (OGP) and phi prime) for the striped venus *Chamelea gallina* from the Huelva coast in southwest (SW) Spain. The morphometric relationship shell height (SH)/shell length (SL) presented isometric growth whereas SL/shell width (SW) and SL/weight (W) displayed negative allometric growth. Shell length at age was estimated through length-frequency distribution (LF) and internal shell growth bands by acetate peel method (AP). The *C. gallina* population consists mainly of three age classes with shell lengths around 13-15 mm for the first year, 25 mm for the second year and 30 mm for the third year. The OGP and phi prime values obtained in the present study are within the range of values for other *C. gallina* populations from the Gulf of Cádiz. Nevertheless, marked differences in growth performance were observed between populations from the Black Sea (lower growth performance) and from other locations along the southern distribution area of this species, which may be related to the low levels of temperature (SST), salinity (SSS) and chlorophyll-*a* (chl-*a*) concentration that exhibit large intra-annual fluctuations.

INTRODUCTION

The striped venus *Chamelea gallina* (Linnaeus, 1758) is a filter-feeding bivalve widely distributed in northeast (NE) Atlantic waters, the Mediterranean Sea and the Black Sea, inhabiting sandy, sandy-muddy and muddy bottoms at depths ranging between 5 and 20 m. *C. gallina* is the main target-species of an important mechanical and hydraulic dredge fishery on the Huelva coast (SW Spain). The volume of catches exceeds 3,000 tons/year with an average landed price of 3-4 €/kg. Catches have dramatically decreased in recent years threatening the biological and economic sustainability of the fishery (Galisteo *et al*. 2012).

The management of a fishery requires information on the state of the stock as well as an accurate estimation of biological and population parameters of the exploited species. Despite the economical importance of *C. gallina* in SW Spain, data on its biology, age structure, growth rates and fishery are scarce. Studies on reproductive aspects (Tirado *et al*. 2002, Rodríguez de la Rúa *et al*. 2003, Delgado *et al*. 2013) or on the state of the fishery in this area (Fernández & Valle 1999, Silva & Juárez 2009) show controversial results with regard to growth parameters.

Environmental variables act on the components of the energy balance equation determining the available energy for somatic growth and/or gonadal development in bivalves (Bayne & Newell 1983). In this sense, there is a direct relationship between ingestion rates and food concentration. In addition, temperature is an important factor that affects the physiology of poikilotherm organisms (Mann 1979). Within limits, an increase of temperature boosts most of the physiological rates, including clearance, ingestion, respiration and growth (Griffiths & Griffiths 1987). Thus, differences in environmental settings throughout the *C. gallina* geographical distribution range may be held partly responsible for dissimilar growth rates at each spot. In fact, preliminary results obtained by our research group (Delgado *et al*. 2014) suggested a study in detail of this topic. In addition, differences in fishing effort are related to differences in the growth of *C. gallina* as Dalgiç *et al*. (2009) described for the Turkish Black Sea coast. This could also be the case between SW Portugal (where only mechanical dredging is allowed) and SW Spain (hydraulic dredge), where significant differences were observed in fishing effort and yield. Age and growth of populations in the Algarve coast (SW Portugal) were estimated by Gaspar *et al*. (2004). However, the dissimilarities on both sides of Cape Santa María in the Gulf of Cádiz (SW Portugal) in terms of oceanography, geomorphology and fishing effort (Navarro & Ruiz 2006; Sánchez *et al*. 2006) suggest a need for an updated study for the *C. gallina* populations from the Huelva coast (SW Spain).

Several ageing techniques have been used to model growth of *C. gallina* populations from the Black Sea (Dalgiç *et al*. 2010), Marmara Sea (Deval & Oray 1998, Deval 2001), Adriatic Sea (Polenta 1993, Arneri *et al*. 1995, 1997, Froglia 2000), Mediterranean Sea (Cano & Hernández 1987; Ramón and Richardson 1992, Ramón 1993) and the NE Atlantic (Royo 1984, Gaspar *et al*. 2004, Silva & Juárez 2009). Among these, analysis of length-frequency distribution, surface growth ring, internal growth lines or mark-and-recapture experiments are the most used techniques.

The purpose of the present study was to estimate the age and growth of a *Chamelea gallina* population off Huelva (SW Spain) using age-length keys estimated by means of size-frequency distribution and acetate peel technique, and to compare the growth performance (both OGP – overall growth performance and ϕ' – growth performance index) obtained in our work with those from literature. Differences on growth performance among striped venus populations distributed throughout the southern part of its geographical distribution range (latitudinal gradient: 37ºS to 43ºN; longitudinal gradient: 10ºW to 35ºE) were discussed based on differences on the environmental conditions, namely sea surface temperature (SST) and salinity (SSS), and chlorophyll-a (chl-*a*).

MATERIAL AND METHODS

Relative growth, shell length-age keys and growth from the Huelva coast: From May 2010 to April 2011, approximately 40 *C. gallina* individuals/month were collected onboard commercial vessels from the Sanlúcar de Barrameda hydraulic dredge fleet at depth ranges of 5-20 m on the Huelva coast (Fig. 1) to study relative growth. Shell length (SL: maximum distance along the anterior-posterior axis in mm), shell height (SH: maximum distance along the dorso-ventral axis in mm) and shell width (SW: maximum distance on the lateral axis, between both valves of the closed shell in mm) were measured to the nearest 0.1 mm with a digital vernier caliper. Whole wet weight (W in g) was obtained with a 0.001 g precision top loading digital balance. Morphometric analysis was performed by estimating the relationships between these variables through the following linear fit (Wilbur & Owen 1964):

$$\text{Log}(Y) = \text{Log}(a) + b\,\text{Log}(X),$$

where Y = SH (SW or W), X = SL, a = intercept (initial growth coefficient) and b = slope or scaling exponent (relative growth rate of variables).

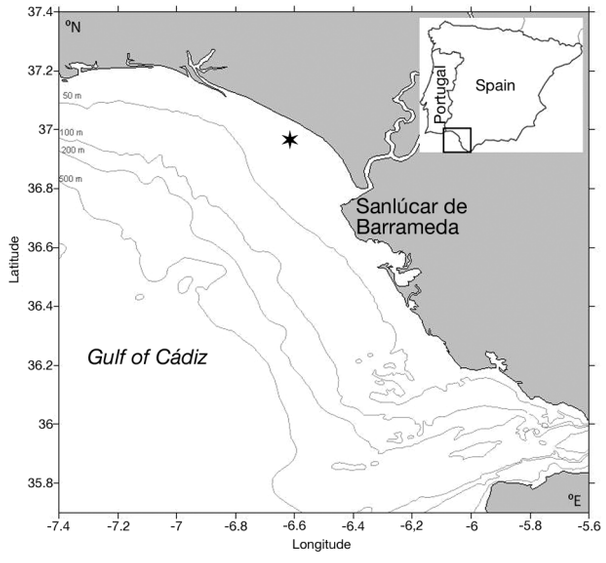

Fig. 1. – Map of the Huelva coast eastward from Sanlúcar de Barrameda (SW Spain). Sampling area (✶).

Shells were then removed from the animal, labeled, and stored to apply the acetate peel technique (AP) later. The present study assumes that *C. gallina* annual growth rings are formed from alternating periods of summer growth and winter quiescence, with seasonal rings being deposited between September and October, as suggested by Gaspar *et al*. (2004). Age at length was estimated from the length-frequency distribution obtained from the analysis of the SL of 2,430 individuals collected just before the expected ring deposition period (August 2010). These were analyzed and a Modal Progression Analysis (Bhattacharya's method) was performed using the computer-based Length-Frequency Analysis (LF) routine of FISAT II software (1.2.2 version) (Gayanilo *et al*. 2002). The threshold value of the separation index was 3 and the Normsep procedure was used.

Bivalves carry a complete record of their lives in their shells (Pannella & MacClintock 1968). Shells contain information of the current age and size and their previous life stages (spat or juvenile phases). An adult can provide several age-length keys since age and size can be obtained from each annual ring. For this reason the largest individuals of each monthly sample were selected to estimate age by means of the acetate peel technique (AP) and a total of 53 individuals with a shell length greater than 30 mm were analyzed to ensure the presence of several annual rings per individual. The left valves were embedded in polyester resin (silastic: polyester, polyurethane and epoxy) prior to sectioning along the anterior–posterior axis, from the umbo to the ventral margin. The sectioned shell surfaces were posteriorly ground, polished and etched in hydrochloric acid (0.01 M). Acetate peel sheets area immersed in ethyl acetate for few seconds, and then placed on the etched shell surface (Richardson *et al*. 1979). After a 1-hour drying period, the acetate is peeled off and sandwiched between clean glass slides for examination in a transmitted-light microscope under low magnification objectives (×10 and ×40), in order to identify seasonal growth rings. For each annual growth ring identified, the distance between the umbo and the RIng was marked and measured using an image analysis software (NIS-Elements AR 3.2). Since these measurements are relative to shell height, data were converted into shell length using the following allometric relationship: $SL = 1.10\ SH^{0.99}$ (derived from 508 shells collected along the study period, $r^2 = 0.995$, $p < 0.01$). Von Bertalanffy growth (VBG) functions were fitted using a non-linear least-squares regression (Gauss-

Newton method; SPSS statistical software, 16.0 version), to estimate the VBG parameters:

$$SL_t = SL_\infty[1 - e^{-k(t-t_0)}],$$

where SL_t = shell length at age t (mm), SL_∞ = theoretical maximum shell length (mm) K = von Bertalanffy growth constant and t_0 = theoretical age at shell length zero (years)

Growth performance indices: Since individual growth is a non-linear process due to the problem of correlation between K and L_∞, the comparison of growth among different taxa in a definite and statistically proper way is difficult (Brey 1999). Growth performance indices can be used to overcome this problem. In addition, several authors (*e.g.* Pauly 1979, Munro & Pauly 1983, Defeo & Cardoso 2004, Lepore *et al.* 2009) demonstrated that growth performance indices are suitable for inter- and intraspecific comparisons. In the present study, the overall growth performance (OGP) and the phi prime index (ϕ') were both applied using the following expressions (Pauly 1979, Munro & Pauly 1983):

$$OGP = \text{Log}\,(KL_\infty^3)$$

$$\phi' = \text{Log}_{10}K + 2\text{Log}10\,L_\infty$$

Both OGP and phi prime were used to compare the growth parameters obtained in our work with other populations of *C. gallina* that occur along the southern part of its geographical distribution area (see Table III and references therein).

Environmental variables: C. gallina growth indices from a heterogeneous set of populations were compared. Since contemporaneous *in situ* observations of comparable instrumental methods were not available, we preferred to use annual mean and annual standard deviation of the monthly means of sea surface salinity (SSS) and temperature (SST), and chlorophyll-*a* concentration (chl-*a*) at the locations indicated in Table III from SeaDataNet (SDN, www.seadatanet.org) Joint Research Activity deliverables. JRA5 provided data for the Mediterranean Sea, the Adriatic Sea and Gulf of Cádiz and JRA6 for the Black Sea. SSS and SST were based on both hydrographic (1900-2007) and satellite (1985-2007) observations whereas chl-*a* concentrations were compiled from SeaWIFS Level-3 maps, all of them distributed as regional SeaDataNet products through its main web portal (http://www.seadatanet.org/Products, accessed on February 2015). Annual means characterized the most significant environmental differences among zones while the standard deviations provided an estimate of the amplitude of the seasonal cycle at each location. Although satellite observations can be biased in nearshore areas, the usage of long-term averages provided a robust approach to assess the most significant environmental dissimilarities among locations. For instance, Navarro & Ruiz (2006) showed that SeaWiFS chl-*a* provides a good approximation for *in situ* chl-*a* observations in the Gulf of Cádiz even in coastal zones.

Principal component analysis (PCA) was used as an ordination method to define a new orthogonal coordinate system to group and describe the multivariate variance in the dataset. *C. gallina* growth performance indices (OGP and phi prime) were analyzed with both annual means and standard deviations of local SSS, SST and chl-*a*. The representativeness of the ordination analysis is given in terms of eigenvalues of the axes and of variance explained by the biplot.

RESULTS

Relative growth on the Huelva coast

The morphometric relationships between shell height (SH), shell width (SW), weight (W) and shell length (SL) are shown in Table I. In terms of SH/SL *C. gallina* presented an isometric growth (b = 1) whereas SW/SL and W/SL showed negative allometric growth (b < 1 and b < 3, respectively).

Length-frequency distribution, internal growth bands and growth performance indices in the Huelva coast

The performance of the Bhattacharya's method allowed decomposing length-frequency distributions into three cohorts (LF), each assumed to represent a separate age class (1, 2 and 3 years old) (Fig. 2). Based on the age-

Table I. – Morphometric relationship parameters for *C. gallina* of Huelva coast (Southwest Spain). SL: Shell length, shell height: SH, shell width: SW, whole wet weight: W. Statistical significance at p < 0.01 (*).

Allometric relation	Log (a)	b	r^2
SH/SL	-0.037	1	0.995*
SW/SL	-0.234	0.972	0.983*
W/SL	-3.301	2.862	0.993*

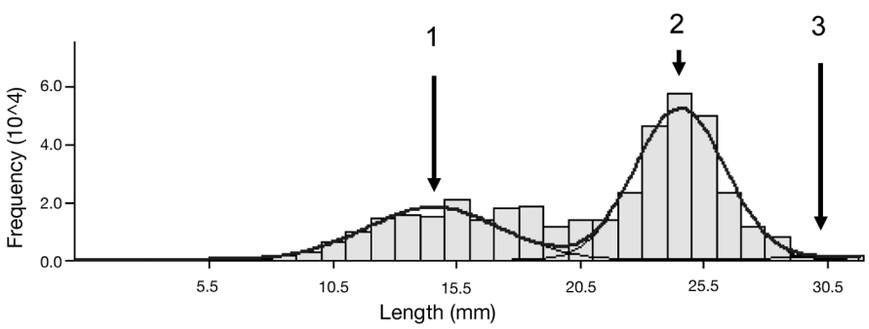

Fig. 2. – Length-frequency distribution for the *C. gallina* population in August 2010. Curves define the cohorts determined by Battacharya's method (1: 1 year, 2: 2 years and 3: 3 years old).

Table II. – Shell length-age key (estimated length (mm) for each year class) and respective standard deviations (± SD, mm) of *C. gallina* from the Huelva coast (SW Spain), obtained from length-frequency analysis (LF) and acetate peel replicas (AP) methodologies.

Method	Age (years)	Mean shell length ± SD	Shell length	
			Min.	Max.
LF	1	14.56 ± 2.73		
	2	24.54 ± 1.83		
	3	30.00 ± 2.91		
AP	1	12.70 ± 3.21	7.97	21.41
	2	25.82 ± 2.64	20.87	32.04
	3	30.45 ± 1.78	26.36	33.02
	4	35.51 ± 1.20	34.14	36.41
	5	37.34 ± 0.80	36.77	37.90

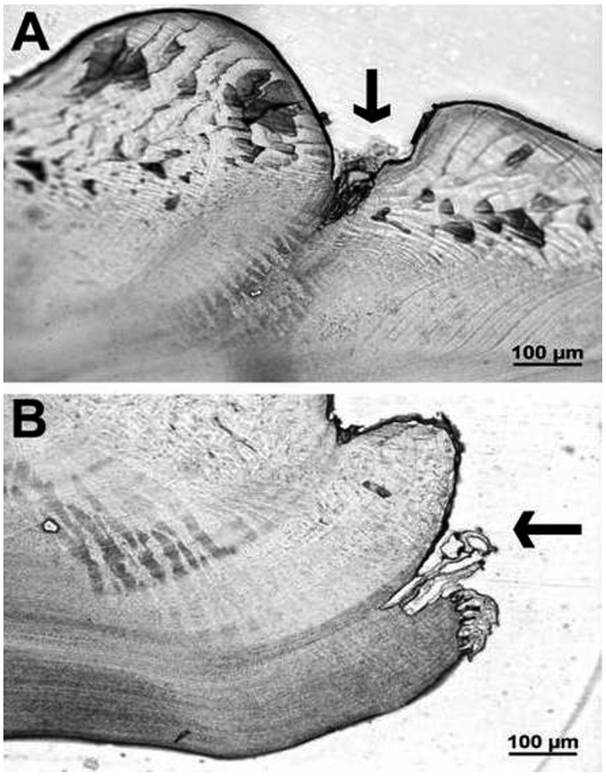

Fig. 3. – Acetate peel replicas of shell sections of *C. gallina*. A: First annual ring (➔); B: Annual ring in the ventral edge of the shell (➔).

length key obtained by this method (Table II) the VBG equation that describes *C. gallina* growth by LF was:

$$SL_t = 44.30\ [1 - e^{-0.38(t + 0.04)}]$$

C. gallina shell growth pattern is printed in the external prismatic layer. Periods of fast growth are characterized by wide translucent zones (growth increments) between growth bands. The narrow deposition of growth bands parallel to the ventral margin of the shell is indicative of slow growth. Progressive aggregation of growth bands result in the narrow and dark growth lines forming the annual ring. Annual rings are often associated with a cleft in the prismatic layer (Fig. 3A and B). In Fig. 3B, the formation of a cleft in the ventral edge can be observed. The mean shell length and standard deviation (± SD) estimated at each year-old class as determined by IB is presented in Table II. Just two of the samples from the fifth-year-old class were read by means of acetate peel replicas methodology, with a mean shell length of 37.34 ± 0.80 mm. The VBG equation that describes *C. gallina* growth by AP was as:

$$SL_t = 36.11\ [1 - e^{-0.79\ (t + 0.45)}]$$

The VBG growth equation obtained using data from LF distributions displayed a higher asymptotic size (L_∞ = 44.30 mm SL) and a lower growth rate (K = 0.38 yr^{-1}) than those obtained from internal growth bands (L_∞ = 36.11 mm SL; K = 0.79 yr^{-1}).

OGP and ϕ' values obtained in the present study using LF distributions were P = 4.519 and ϕ' = 2.873, respectively, whilst when age was estimated using the micro-growth patterns in shell sections OGP was 4.571 and ϕ' was 3.013.

Environmental setting along the southern distribution area of C. gallina

The Black Sea and Marmara Sea show the lowest mean salinities, below 23 psu and about 18 psu, respectively. The Gulf of Valencia shows typical Mediterranean surface salinities greater than 37.7 psu. In contrast, the Ancona and Neretva waters (Adriatic Sea) exhibit relatively lower mean salinities (about 36 psu in Ancona and around 37.5 in Neretva waters). The Gulf of Cádiz is dominated by fresher North Atlantic surface waters of about 36 psu. The Marmara Sea exhibits the largest intra-annual variability, featuring a seasonal cycle of surface salinities with high salinities being observed in February-March (about 25 psu) and low salinities being registered in August (about 20 psu; SD > 1.2 psu). However, surface salinities are rather stable in the Black Sea and the Gulf of Valencia throughout the year (SD about 0.1 psu). Although without a clear seasonal cadence, the eastern Gulf of Cádiz (Huelva coast) and the Adriatic locations exhibit larger intra-annual variability (SD > 0.35 psu) (Table III and Fig. 6A).

The Black Sea and the neighboring Marmara Sea exhibit the lowest SST (< 16 ºC) values. In contrast, SST is above 17.5 ºC elsewhere, with maximum values in the western Mediterranean coast (about 19 ºC). All sites are subjected to an in-phase thermal seasonal cycle, with August being the warmest month and February-March the coldest. This seasonal cycle show smaller amplitude in the Atlantic zones (SD of 2-3ºC) as compared with the Mediterranean (SD > 4 ºC) and the Marmara and Black Sea (SD about 6 ºC) (Table III and Fig. 6B).

Mean surface chl-*a* concentrations also indicated strong differences between the studied areas. The largest values are observed in the eastern Gulf of Cádiz (Huelva

Table III. –Values of von Bertalanffy growth constant (k), theoretical maximum shell length (L_∞) and growth performance indices (OGP and phi prime) estimated for *C. gallina* populations by several authors. Annual mean value and standard deviation (SD) of SSS (psu), SST (ºC) and chl-*a* concentration (mg/m^3) in the different population sites. Ageing method: LF, length frequency; SR, surface rings; AP, Acetate peel; TS, thin sections.

Ref.	Method	K	L∞	OGP	phi prime	Latitude	Longitude	Study area	Author	Mean SSS ± SD	Mean SSD ± SD
Alg	AP	0.47	38.95	4.444	2.853	37°4'N	8°7'W	Faro (Atlantic Ocean, Portugal)	Gaspar *et al.* (2004)	36.15 ± 0.14	18.04 ± 2.29
Alg	LF	0.32	42.15	4.380	2.755	37°4'N	8°7'W	Faro (Atlantic Ocean, Portugal)	Gaspar *et al.* (2004)	36.15 ± 0.14	18.04 ± 2.29
Alg	SR	0.71	37.55	4.575	3.000	37°4'N	8°7'W	Faro (Atlantic Ocean, Portugal)	Gaspar *et al.* (2004)	36.15 ± 0.14	18.04 ± 2.29
Hue	AP	0.79	36.11	4.571	3.013	37°0'N	6°35'W	Huelva (Atlantic Ocean, Spain)	Present study	36.00 ± 0.35	18.51 ± 3.05
Hue	LF	0.38	44.30	4.519	2.873	37°0'N	6°35'W	Huelva (Atlantic Ocean, Spain)	Present study	36.00 ± 0.35	18.51 ± 3.05
GoV	AP	0.35	36.12	4.217	2.660	39°09'N	0°13'W	Gulf de Valencia (Mediterranean Sea, SE Spain)	Ramón and Richardson (1992)	37.81 ± 0.09	18.99 ± 4.65
GoV	LF	0.40	40.05	4.410	2.807	39°30'N	0°17'W	Gulf de Valencia (Mediterranean Sea, SE Spain)	Ramón and Richardson (1992)	37.81 ± 0.09	18.99 ± 4.65
AdW	AP	0.21	52.220	4.475	2.758	43°37'N	13°31'E	Ancona (Adriatic Sea, Italy)	Polenta (1993	36.31 ± 0.50	17.49 ± 5.29
AdW	TS	0.48	41.60	4.539	2.919	43°37'N	13°31'E	Ancona (Adriatic Sea, Italy)	Arneri *et al.* (1995)	36.31 ± 0.50	17.49 ± 5.29
AdE	TS	0.52	39.50	4.506	2.909	43°00'N	17°25'E	Neretva estuary (Adriatic Sea, Croatia)	Arneri *et al.* (1997)	37.50 ± 0.44	18.48 ± 4.30
Mar	SR	0.43	34.17	4.234	2.701	40°58'N	28°58'E	Northern Marmara Sea (Turkey)	Deval and Oray (1998)	22.27 ± 1.23	15.52 ± 6.38
Mar	AP	0.37	33.46	4.142	2.617	40°58'N	28°58'E	Northern Marmara Sea (Turkey)	Deval (2001)	22.27 ± 1.23	15.52 ± 6.38
BSE	TS	0.16	26.00	3.449	2.034	41°37'N	35°32'E	Yakakent (Black Sea, Turkey) (Y)	Dalgiç *et al.* (2010)	18.00 ± 0.13	14.74 ± 5.80
BSC	TS	0.21	28.88	3.704	2.243	42°01'N	34°54'E	Inceburun (Black Sea, Turkey) (I)	Dalgiç *et al.* (2010)	18.00 ± 0.11	14.55 ± 5.83
BSW	TS	0.22	26.60	3.617	2.192	41°53'N	32°56'E	Cide (Black Sea, Turkey) (C)	Dalgiç *et al.* (2010)	18.02 ± 0.13	14.68 ± 6.05

coast) and the Marmara Sea (> 4 mg m^{-3}), followed by Ancona (Adriatic Sea) and the western Gulf of Cádiz (> 1.5 mg m^{-3}). Lowest mean chl-*a* concentrations are observed in the Neretva estuary (< 0.2 mg m^{-3}) followed by the easternmost Black Sea locations and the Gulf of Valencia (< 1 mg m^{-3}) (Table III). Most of the intra-annual chl-*a* variability was primarily driven by a strongly site-dependent seasonal cycle. For instance, the Marmara Sea showed a single maximum in April (up to 9 mg m^{-3}) and a minimum in August (< 2 mg m^{-3}) whereas the Gulf of Cádiz presented two well- defined annual maxima (April and November) with a single annual minimum (in Summer from June-September, depending on the location within the Gulf) (Fig. 6C). Of these, the Marmara Sea showed a larger seasonal variability (SD > 2.5 mg m^{-3}) whereas in spite of the relatively high concentrations, the eastern Gulf of Cadiz exhibited relatively moderate annual variations (SD < 1 mg m^{-3}) (Table III) suggesting the presence of relatively high chl-*a* levels throughout the year.

Growth indices were correlated with the environmental observations after computing a matrix of Pearson's r correlation coefficients and by applying a principal component analysis (PCA) using either OGP or phi prime as biotic factor and SST, SSS, chl-*a* together with their corresponding standard deviation as abiotic factors. PCA results were similar in both cases and therefore only the phi prime case is presented here (Fig.7). PCA grouped the study areas as a function of the environmental setting and *C. gallina* growth indices. Two components had eigenvalues ≥ 1 with the first component (PC1; 51.8 % explained variance) related to SSS, SST and its intra-annual variability. These results agree with Pearson's correlation coefficients shown in Table IV. The second component aggregated chl-*a* concentration, its variability, SSS variability and the growth index (PC2; 37.2 % explained variance). The PC1 had a strongly positive correlation with SST, SSS and a negative correlation with SST seasonal cycle. Along this PC1, the Black Sea and Marmara Sea case studies were clearly distinct from the Mediterranean and Atlantic ones, the former featuring low salinity and temperature values and strong seasonal thermal cycle. PC2 also permitted to further separate the Marmara from Black Sea cases. The former exhibited relatively high phi

Table IV. – Pearson rank order correlation (r) between environmental variables and growth indices. Significant correlations at $p < 0.05$, $p < 0.001$ (**) and at $p = 0.000$ (**).

	Phi prime	OGP
SSS	0.85**	0.88***
SST	0.82**	0.83**
chl_*a* concentration	0.28	0.25
SSS_SD	0.15	0.14
SST_SD	-0.61*	-0.59*
chl_*a*_SD	0.14	0.14

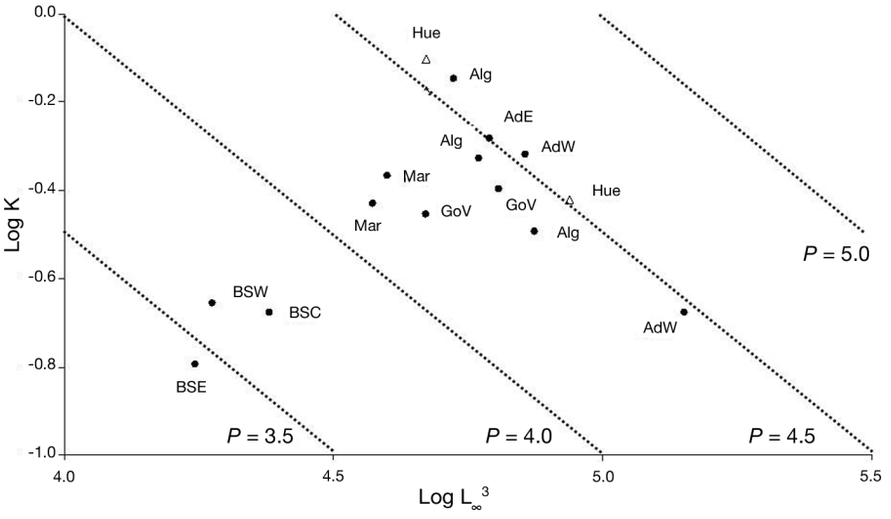

Fig. 4. – Overall growth performance (OGP, noted as P) obtained for *C. gallina* populations. Diagonal lines in the auximetric grid indicate equal values of OGP. Acronym references: Alg, Algarve; Hue, Huelva coast; GoV, Gulf of Valencia; AdW, Ancona; AdE, Neretva estuary; Mar, Northern Marmara Sea; BSE, Yakakent, eastern Black Sea; BSC, Inceburun, Central Black Sea; BSW, Cide, western Black Sea. Open triangles correspond to the present study.

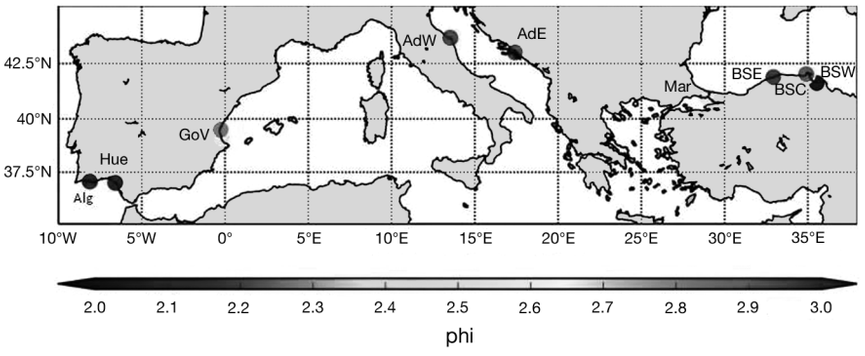

Fig. 5. – Phi prime index values map obtained for *C. gallina* populations along the southern part of its geographical range. Acronym references: Alg, Algarve; Hue, Huelva coast; GoV, Gulf of Valencia; AdW Ancona; AdE, Neretva estuary; Mar, Northern Marmara Sea; BSE, Yakakent, eastern Black Sea; BSC, Inceburun, Central Black Sea), BSW, Cide, western Black Sea.

prime, high annual mean chl-*a* concentrations and high SSS and chl-*a* variability whereas the latter featured lower phi prime, lower chl-*a* concentrations and weaker interannual SSS and chl-*a* variability. Similarly, the Adriatic Sea zones (Ancona and Neretva estuaries) and the eastern Gulf of Cádiz (Huelva coast) could be segregated from the Gulf of Valencia and the Algarve populations.

DISCUSSION

Relative growth, shell length-age keys and growth of C. gallina *in the Huelva coast*

The fact that Huelva coast *C. gallina* displayed an SH/SL isometric growth is in accordance with previous works (Valli & Zecchini-Pineisch 1982, Cano & Hernández 1987, Ramón 1993), but differs from Gaspar *et al.* (2002) results for the Algarve coast, where there is a positive allometric relationship which may be related to differences on the sediment type, more silty in the Huelva area than in Algarve. Huelva coast *C. gallina* exhibited negative SW/SL and W/L allometric growth, in agreement with the findings of Gaspar *et al.* (2002) in the Algarve and Ramon (1993) for the Mediterranean Sea.

Concerning age assignation methodologies, the present paper presents the second estimation of growth parameters in an Atlantic population using the acetate peel technique. The shell length-age-keys obtained by the two methods (LF and AP) showed a slight difference in the shell length assigned to the first year. Differences between methodologies were more considerable among the growth curves fitting, and a maximum asymptotic shell length (L_∞) of 44.3 mm was observed using the LF instead the AP technique. In this context, Seed (1976) advised against the use of the length-frequency distribution to estimate growth rate for population characterized by extensive spawning period, high individual growth rate and short lifespan as is the case of *C. gallina* (Delgado *et al.* 2013).

The AP technique allowed the identification of the growth pattern in the prismatic layer of the shell. The growth curves estimated on the Huelva coast indicated that *C. gallina* grows relatively fast the first two years, but slows down afterwards. Occasionally individuals of fourth and fifth-year-old classes were sampled. Therefore, *C. gallina* population consists of three age classes with lengths around 13 mm for the one-year-old, 25 mm for the second-year-old and 30 mm for the third-year-old classes. Since the minimum landing size for this species is 25 mm, fishing effort is exerted over the second and

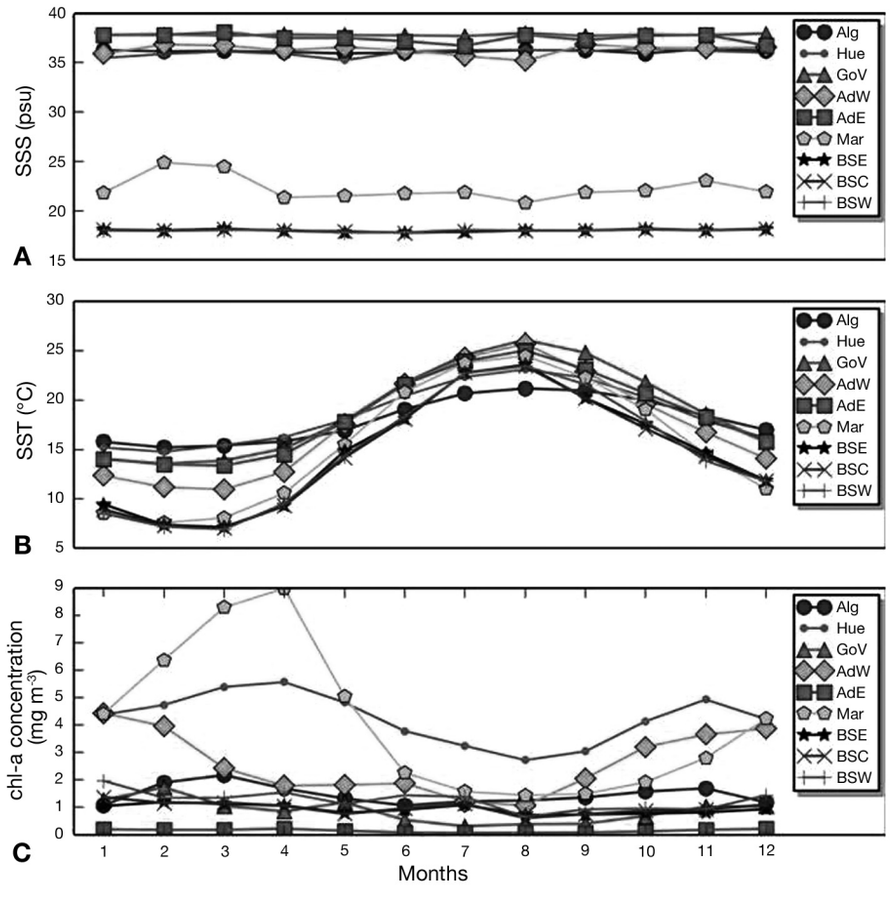

Fig. 6. – Seasonal cycles of sea surface salinity (SSS) (A); Sea surface temperature (SST) (B); and chlorophylll-*a* concentration (chl-*a*) (C) from the different *C. gallina* population sites. Acronym references: Alg, Algarve; Hue, Huelva coast; GoV, Gulf of Valencia; AdW Ancona; AdE, Neretva estuary; Mar, Northern Marmara Sea; BSE, Yakakent, eastern Black Sea; BSC, Inceburun, Central Black Sea), BSW, Cide, western Black Sea.

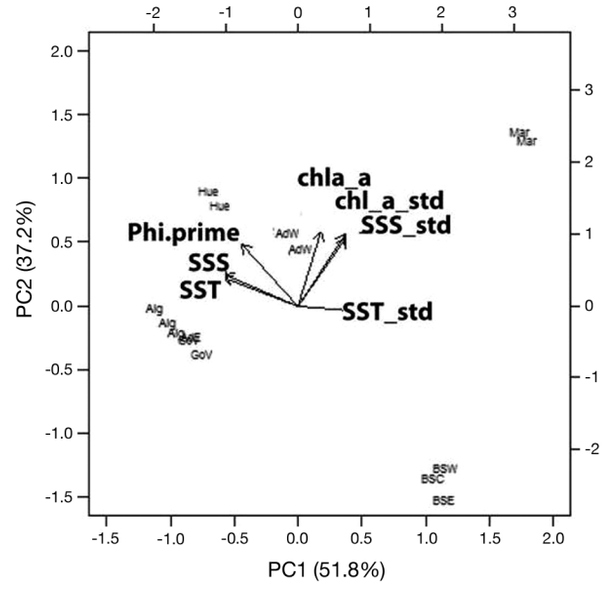

Fig. 7. – Principal Components Analysis (PCA) biplots of sea surface salinity (SSS), sea surface temperature (SST), chlorophyll-*a* concentration (chl-*a*) and their standard deviation (SSS_SD, SST_SD and chl_*a*_SD) as abiotic factors, and phi prime index as biotic factors.

third age classes of this population in this zone of the Gulf of Cádiz.

Growth performance indices of C. gallina

The OGP values obtained in the present study are within the range of values reported by other authors for *C. gallina* populations from Algarve, the Mediterranean and Adriatic zones (Fig. 4 and Table III). Indeed, the OGP for most of these *C. gallina* populations fall around 4.5. An OGP gradient was observed from west to east (with the exception of the Adriatic sea). Similarly to OGP, the phi prime values determined in the present study are consistent with those previously estimated by Gaspar *et al.* (2004) for the population from the Portuguese zone of the Gulf of Cádiz. Consequently growth parameters presented in this study are an accurate representation of the considered population, since phi prime values must be similar for the same species occurring in similar areas (Munro & Pauly 1983, Brey 1999, Bellido *et al.* 2000). Throughout a large geographical domain phi prime values of the populations studied by other authors are grouped by zones and, notwithstanding phi prime values, seem to decrease from the NE Atlantic towards the extreme eastern Mediterranean with similar values being grouped in neighboring, environmentally similar, zones (Fig. 5). Several authors observed a relationship between growth and latitude (*e.g.* Gutierrez and Defeo 2003, Fiori & Morsán 2004, Moura *et al.* 2009). However, in the present study the popula-

tions analyzed are distributed throughout a narrow latitudinal range and therefore the influence of latitude cannot explain the differences on the growth among stripped venus populations. The gradient observed is apparently longitudinal and is related to the environmental characteristics of each NE Atlantic and Mediterranean areas.

Variations on growth indices and their relationship with environmental variables

Environmental variables act simultaneously on bivalve growth and the way that these factors affect each of the physiological rates that integrate the energy-balance equation determines the amount of energy available for growth or reproduction (Bayne & Newell 1983).

PCA was able to satisfactorily group population growth performance as a function of the oceanographic settings. These results showed that the Black Sea and Marmara Sea case studies were significantly different from those located further west. However, the apparent longitudinal variation of growth performance indices appears to be related to oceanographic settings of each area. The Black Sea and Marmara Sea featured low salinity and thermal values and a strong seasonal thermal cycle. In the case of the salinity, this seems to be a consequence of the local positive freshwater balance and its propagation into the Mediterranean basin through the Marmara Sea. In addition, low levels of chlorophyll-*a*, phi prime index and chlorophyll-*a* and salinity variability differentiated Black Sea areas from Marmara Sea. The rest of areas showed higher values of salinity and temperature, but a slight thermal variability. The Huelva coast and the western Adriatic Sea areas displayed higher levels of chlorophyll-*a* and more variability than the other occidental areas.

With regard to salinity, some authors have described reductions in the clearance and ingestion rates of bivalves such as *Argopecten purpuratus* (Fernández-Reiriz *et al*. 2005, Navarro & González 1998) or *Mytilus edulis* (Bohle 1972) with low salinity. In fact, our results are in accordance with these findings and the growth performance indices of *C. gallina* were positively related with salinity and negatively with its variability. The low feeding activity and the relative high energy lost by excretion and respiration resulted in a negative scope for growth in *A. purpuratus* (Navarro & González 1998). Nevertheless, these authors also point out that the physiological responses recorded at lower salinities can be transitory and the magnitude of the changes would be time-dependent over longer timespans. In fact, *C. gallina* is an euryhaline species and has a high capacity to acclimatize to extremely brackish conditions, which may explain its abundance along these areas (Dalgiç *et al*. 2010, Deval 2001).

Temperature also plays an important role on bivalve growth as our PCA results suggest. Phi prime indices were positively correlated with SST and negatively correlated with SST seasonal cycle. This suggests that relatively high year-round temperature is beneficial for positive venus clam growth. Within non-lethal margins, temperature affects physiological rates (*e.g*. ingestion or respiration rates) and is positively correlated with growth rates of marine invertebrates (Bayne & Worral 1980).

Food availability (proxy-ed by chl-*a* concentration), which determines ingestion and consequently the total amount or energy absorbed by the clam, is also an important limiting factor for growth in marine poikilotherms (Albentosa *et al*. 1994). Chl-*a* concentrations seemed to give the key for the segregation of neighboring populations in the Gulf of Cádiz. The Huelva coast in the eastern Gulf of Cádiz showed year-round, relatively high chl-*a* concentrations, as compared with the Algarve case, just 50 miles further west (Navarro & Ruiz 2006). Nevertheless, the influence of food concentration on physiological parameters must be studied carefully in a context where the temperature plays an important role. Phi prime results presented here did not show differences from site to site except for the Black Sea and Marmara Sea that featured extremely low phi prime values.

The case of the Gulf of Cádiz populations is special since the dissimilar environmental settings between eastern and western zones do not correspond with different phi prime values. This suggests that feeding and metabolic rates may increase up to an optimum with favorable temperature and food concentration, beyond which there is a relative decline, as indicated by Griffiths & Griffiths (1987). Laboratory experiments show that an increase in temperature (from 18 to 22 ºC) leads to an increase in energy consumption and a subsequent decline in the energy balance in *Ruditapes philippinarum* (Delgado & Pérez-Camacho 2007). *In situ C. gallina* growth response to SST alone cannot be isolated from the combined effects with chl-*a* concentration. High chl-*a* concentrations and the stronger seasonal thermal cycle (and probably the combination of both) on the Huelva coast could be beyond the optimum threshold for this species, what could explain the absence of differences in growth performance with the neighboring Algarve populations. Nevertheless there are no physiological studies about the energy balance of *C. gallina* under different environmental conditions or about these optimum thresholds to confirm this hypothesis.

The strong difference in growth performance observed between *C. gallina* populations in the Black Sea and those located elsewhere could also be explained by their exposure to dissimilar temperature ranges and the effects of this on the construction of the shell. The solubility of calcium carbonate increases with decreasing temperature (and increasing pressure) and the metabolic cost of the construction of shell material is greater at low temperatures (Dietrich *et al*. 1980, Clarke 1983). Vakily (1992) reported a linear increase of growth performance indices with the mean annual temperature for Mytilidae. This author also suggested that warm-water species are able

to produce more shell material during their growth period than their cold-water relatives. This seems to correspond with observations taken from the Black Sea (in the eastern limit of distribution, Gofas *et al*. 2011), whose *C. gallina* populations exhibited the lowest growth performances under the coldest conditions. In addition, the Black Sea is characterized by relatively low chl-*a* concentration, and therefore food availability could be another limiting factor for local growth performance.

To sum up this study, we attempted to understand how the different combinations of thermohaline conditions and food availability influence *C. gallina* growth performance in southern European populations. A comparative analysis of a number of case studies reported in literature and new estimations presented here was carried out. The analysis suggests that the lowest growth performances featuring Black Sea populations were related to low temperature, low salinity and low chl-*a* that exhibit large intra-annual fluctuations. In contrast, the highest growth performances observed in the Gulf of Cádiz occur in parallel with higher temperature (but also with a reduced seasonal range), salinity and chl-*a* concentration. In the absence of dedicated laboratory studies for *C. gallina*, the spatio-temporal match-mismatch of favorable conditions (in terms of an adequate temperature regime, sufficient food availability and fishing effort and other predatory pressures) makes it difficult to unravel their combined effects from the study of *in situ* populations alone. Further studies should be conducted in order to investigate the combined effects of all these on growth rates, spatial distribution, abundance and population structure of this species. These studies will be of particular interest for the assessment of *C. gallina* from the market-demanding Gulf of Cádiz stock.

ACKNOWLEDGEMENTS. – We thank E Martínez for her valuable technical assistance. We thank our colleagues at IEO (Centre of Cádiz), especially A Juárez, and the observers on board who collaborated in the biological sampling and sample analysis, as well as the owners and crew of the fishing vessels from which the samples were obtained. Thanks are also due to the anonymous referee whose suggestions greatly improved the final version of the manuscript. This study was carried out within the framework of the project: "Análisis de la población de chirla, como especie de interés pesquero, en la reserva de pesca de la desembocadura del río Guadalquivir" funded by the Consejería de Agricultura y Pesca (Junta de Andalucía - European Fisheries Fund) in collaboration with the Instituto Español de Oceanografía.

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Received on June 25, 2014
Accepted on November 16, 2015
Associate editor: G Tita